On the Presence of Nasal Secretory Sacs and a Naso-pharyngeal Communication in Teleostei, with especial reference to *Cynoglossus semilævis*, Gthr. By H. M. Kyle, M.A. (Communicated by Prof. G. B. Howes, Sec. Linn. Soc.)

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(Plate 38.)

The observations embodied in this paper have been made during the course of a prolonged research into the anatomy of the Flat-fishes (Heterosomata). It is considered advisable to publish them separately because, though the research is far from completed, the facts to be described have a certain importance apart from the main series of results. In order to carry on my work successfully I spent some time at the British Museum of Natural History, and I desire to acknowledge my indebtedness to Mr. G. A. Boulenger, F.R.S., of the Zoological Department of that Institution. Every facility was given to me for my work, and his advice, generously offered, has aided me in many directions. I am proud to acknowledge also the friendly counsel and masterly criticism of Prof. G. B. Howes, F.R.S., to whom indeed the appearance of this paper in its present form is due.

It is generally believed and taught that Fishes possess no secretory apparatus in connection with their olfactory organs, and that in the Teleostei these organs have no direct communication with the mouth. These characters, and more especially the latter, have been considered as almost exclusively distinctive of the air-breathing Vertebrates—so much so that Huxley, in his famous paper on *Ceratodus Forsteri* *, discussing the communication present in the Dipnoi, considered it necessary to raise and answer the question—of what use are "internal nares" to purely branchiate animals? Internal nares in water-breathing vertebrates seem indeed unnecessary, because the respiratory apparatus is in immediate communication with the mouth, so that where they do occur a special explanation has to be sought. As with the Dipnoi and *Myxine*, so with the case to be herein described, the function of the naso-pharyngeal communication seems quite clear, though its presence may run counter to our preconceived notions.

* Proc. Zool. Soc. 1876, *cf.* pp. 24 & 180.

In order to obviate a confusion of terms which might readily arise in dealing with the subject of this paper, I shall refer to the organ of smell as the *olfactory organ*; to certain accessory derivatives of that organ as *nasal sacs*; to the one or two external apertures of the olfactory organ of the Teleostei as *anterior* and *posterior nostrils*; and to the apertures and passages of communication between the nose and the mouth as the *posterior* or *internal nares*.

The existence of nasal sacs in connection with the olfactory organs of Teleostei has been noted by Owen, who in 'The Anatomy of Vertebrates' (p. 329) mentions their occurrence in the Mackerel (*Scomber scombrus* L.) and in the Wolf-fish (*Anarrhichas lupus*, L.). In the latter he states that the "reservoir passes backward (expanding) as far as the back part of the palate, where it ends blindly;" and adds, "the prolongation of the single nasal cavity in the Lamprey is analogous to this." Although Owen* mentions the Mackerel as possessing these reservoirs, they are comparatively slightly developed. Solger† has more recently discovered a similar organ in the Stickleback.

These are not the only species, however, where such "reservoirs" occur. They are met with in those forms which lead a semi-sedentary life—in the Blenniidæ, and (more largely developed) in the Labridæ and Scorpænidæ. Sometimes there are two "sacs" in connection with each olfactory organ—Scorpænidæ; sometimes only one—Blenniidæ and Labridæ.

These sacs are simple continuations of the nasal cavity and possess no secretory function. They are "reservoirs" as Owen called them, associated with the retaining, circulation, and changing of the water which passes through the nostrils. Their walls are not muscular, and their capacity is determined merely by the movements of the ascending processes of the premaxillæ and the maxillæ and palatines. Solger suggests that they may also furnish a habitat and breeding-place for Infusoria!

A further specialization of the nasal sacs is found in certain groups of flat-fishes, and here also the number present for each olfactory organ varies—in the Halibut, Plaice, and Turbot

* Milne-Edwards also states that the nasal organ in the Mackerel possessed a 'cul-de-sac.' Leç. sur la Physiologie et l'Anat. Comp. tom. xi., 1877, p. 476.

† Solger, B.: "Notiz über die Nebenhöhle des Geruchsorgans von *Gastrosteus aculeatus*, L." Zeit. für Wiss. Zool., Bd. 57, 1894, p. 186.

there are two, in the Sole tribe only one, in the aberrant Sail-fluke (*Lepidorhombus whiff*) none at all. In the Halibut, Plaice, and Turbot tribes, when the sacs are developed they lie anterior to the ethmoid, and are closely connected with the pterygo-palatine and maxillary bones (Pl. 38. fig. 1, $n.s._1$–$n.s._4$). In the genus *Solea* that of the right or eyed side also lies anterior to the ethmoid, whilst that of the left or blind side extends posteriorly over the roof of the mouth to as far back as the posterior third of the parasphenoid (fig. 2, *l.n.s.*). In the above-mentioned groups the function of these sacs is entirely secretory, their blind ends resting on a layer of fatty tissue immediately over the integument lining the roof of the mouth (fig. 1, *f.t.*). In the genus *Solea* the larger, posteriorly directed sac acts for the most part as a reservoir just as in the cases cited. A small quantity of mucus is certainly always found in it, but mixed with a large percentage of sea-water.

In order to render fully clear the significance of these facts, it is necessary to state the correlated differences in form and structure of the several species of flat-fishes. This would lead too far away, however, from the subject at present in hand, and it need only be said that the Soles are better adapted for more sand-loving habits than are the Halibut, Plaice, and Turbot.

Leaving the physiological significance of these sacs for discussion later, we may turn now to a remarkable form first described by Dr. Günther *, a native of the China Seas, and called by him *Cynoglossus semilævis*. This species is included under a sub-family of the Sole group, but is well marked off from the true Soles, and is probably of separate origin. In European waters it has a near ally in the small *Ammopleurops* (*Plagusia* of the French ichthyologists) of the Mediterranean. The characteristics of the true Soles—the curved snout projecting in front of the mouth, the small eyes and largely developed olfactory organs, the slender and slightly developed opercular bones with contours completely hidden by the skin, the comparatively small branchial openings, and various other internal peculiarities of skull and skeleton—are accentuated in *Cynoglossus*, and indicate a greater adaption to sand-loving habits than is found even among the true Soles. The degeneration of the fins evidenced in these latter reaches its extreme. The pectoral fins have entirely

* Ann. & Mag. Nat. Hist. ser. 4, xii. 1873, p. 379, and ser. 7, i. 1898, p. 261.

disappeared and one ventral only remains, the dorsal and anal are continuous round the tail, and the tail itself, carrying further the change begun in *Solea*, has become "pseudo-diphycercal."

These characteristics give the impression not merely of sand-loving habits, but also that the animals bury their comparatively heavy jaws and snout in the sand or gravel, whilst their long, slender, and flexible tails move freely in the water. And in this position they are more dependent upon their sense of smell than upon their powers of sight for the detection of their food.

Correlated with their mode of life in some mysterious way is the peculiar development of their lateral-line system. On the right or blind side there is only one lateral line, on the left or eyed side there are three of them—one median, the other two near the bases of the dorsal and anal fins. The median and dorsal lines are continued on to the head, over the occipital region of which a connecting branch joins the two. The median line gives off the usual branch over the preoperculum to the mandible, and continues forward almost to the anterior border of the head, where it joins the dorsal line, which has followed the contour of the head and is continued round the border to the curved snout.

Five specimens referred to this species, *Cynoglossus semilœvis*, have been examined, one of them in detail, the other four only with regard to certain doubtful points *. Although these are classed by Dr. Günther as representatives of one species, the individual examined in detail differs so markedly from the other four that some systematists would not hesitate to make it the type of a separate species or even genus, and the advisability of this will be considered when the facts concerning it have been described.

The characters already enumerated are shared by all five, and in external appearance there is only one point of difference between the divergent specimen and the others. In it, an accessory branch of the lateral line passes backward from the ring round the snout towards the posterior nostril between the eyes. In the others this is absent. It is difficult to say what value can be put upon this character. In many nearly allied species, e. g. *Synaptura*, it is in exactly the same position; and in many of the North American flat-fishes (especially on the Pacific coast)

* As these were registered specimens, I was very fortunate in having so many to examine and in being permitted to handle them so fully.

Jordan* describes an accessory branch of the lateral line as passing backward from the head along the back of the dorsal fin. It is connected with other peculiarities, and must have some relation to the mode of life of the different species; and in the case of *Cynoglossus* it is present along with certain characters which plainly show the greater adaptation of its possessor to more sand-loving habits than those which do not have it.

In the case of *Solea*, it has been said that one of the nasal sacs extends backward over the roof of the mouth, whilst the other is quite separate and lies anterior to the ethmoid. In the four specimens of *Cynoglossus*, so far as could be ascertained by means of a seeker without actual dissection, there is a single large sac lying over the roof of the mouth, resembling in position the large posteriorly directed sac of *Solea*. Into this both nasal canals open—one from each nasal cavity. The nasal organs, which are placed symmetrically on each side of the head, are thus in communication with a large "cul-de-sac" which occupies the entire area overlying the median portion of the roof of the mouth.

The step is not great from this combination to that found in the divergent specimen. The roof of the mouth in this is perforated by a large oval opening (Pl. 38. figs. 3, 4, 5, *c*), around which the mucous membrane is thrown into a broad rim or fold, projecting inward and underlying a portion of the central chamber, which in position corresponds to that enclosed by the sac of the other four specimens. When this rim is cut through anteriorly, two comparatively large openings are seen (fig. 5) —one on each side of the median line. These lead into the nasal canals which pass upwards and forwards—one on each side of the parasphenoid—internal to the palatines, until they reach positions anterior to and alongside of the ethmoid, and open at their upper extremity into the posterior portion of the nasal cavities (fig. 3, *e*). On the eyed side of the head the canal passes downward from the nasal cavity close to the membranous lining of the lower orbit (fig. 3, *n.p.c.*). These canals are tolerably large, and form an effective means of communication from the exterior, through the nasal cavities, to the mouth.

* Jordan, D. S., & Goss, D. K.: "A Review of the Flounders and Soles (Pleuronectidæ)," Rep. U.S. Comm. of Fish and Fisheries, 1886.—Jordan, D. S., & Evermann, B. W.: 'The Fishes of North and Middle America,' 1898.

The other structures in connection with the mouth vary little in the different specimens. In all, the jaws of the upper (eyed) side are quite bare, whilst those of the lower (blind) side display strong series of chisel-shaped teeth (fig. 3, *t.m.*). The mandibular and maxillary "breathing-valves" * are strongly developed (fig. 4, *b.v.*), and the only appreciable difference is seen in the length of the gill-filaments. These are very long in all specimens, exceeding the usual length found in the Heterosomata, but are slightly longer in the divergent specimen than in the others. Although dissections of four of the specimens were not made, it is most probable that in other characters of the head and body all five are alike, since by analogy I find in the Plaice and Flounder, in which the internal structure differs little, that what important differences there are may be seen externally.

The question then presents itself whether the single specimen of *Cynoglossus* is entitled to be taken as the type of a new species. It is possible, indeed, that such a species really exists, because if this peculiar combination of characters occurs in one individual, there is no reason why it should not occur in many others. On the other hand, it is possible that this individual may be quite unique, and that the accessory portion of the lateral line and the increased length of the gill-filaments may have arisen after the perforation of the roof of the mouth in the life-history of it alone; but this does not seem very probable. The lateral line in other forms is developed at a very early stage, and if an accessory branch is present, we should imagine that it would arise about the same time as the main portions. Hence the perforation of the roof of the mouth must have appeared in the earlier stages of life; and, if so, is possibly inherited—that is to say, a distinct species may exist whose characters are fairly constant and reappear in the offspring. It is possible again that we have here only the beginning or the foreshadowing of a new species. If we reason from the principle of Natural Selection, we may conclude that the possession of a naso-pharyngeal communication would result in great advantage to a fish living in the sand. Or we may say, with Dohrn †, that the change in

* Owen, R.: 'Anatomy of Vertebrates,' vol. i. p. 413.—Dahlgren, W.: "The Maxillary and Mandibular Breathing-valves of Teleostean Fishes," Zool. Bull. Boston, 1898. Smitt, F. A.: 'Scandinavian Fishes,' p. 263.

† Dohrn, A.: 'Das Princip des Functionswechsels.' Leipzig, 1874.

function, from secretory to water-retaining, being accompanied by changes in the tissues, may have led to a great change in structure, and that Natural Selection has been thereby confronted by variations which it will convert into specific differences. Or, discarding Natural Selection and questions of "advantage" and "survival of the fittest," it seems simpler and more natural to believe that the remaining longer than usual with the head buried in the sand, *i.e.* a slight change in habit*, may have brought about the perforation of the roof of the mouth, in which case the presence of the naso-pharyngeal communication, accompanied by the change of habit and habitat, would have a "discriminative" as distinguished from a "selective" value.

Whichever way the matter be argued, we see how this important "modification" gives us the possibility of a new species, although it is better perhaps to wait for additional evidence before recording it as such in the classification of the Heterosomata.

The discovery of a naso-pharyngeal communication in only one specimen so far does not, however, lessen the interest attaching to its presence. Such facts are rare in the class Pisces, so that, when they do occur, their general importance is so great as to render the question of their specific value a somewhat secondary matter. The importance and interest do not lie in the uniqueness of this single individual, but in the occurrence in the Teleostei of on organ hitherto unknown in them and considered as almost peculiar to the air-breathing Vertebrates.

We may now turn our attention to more general considerations, and in the first place to those of function. The first stage, or most elementary condition, where "reservoirs" with water-retaining functicn are present among Fishes, is found in *Labrus*, *Scorpæna*, *Gastrosteus*, and *Anarrhichas*, but it is absent in the Gadidæ so far as examined, as also in the Herring. These sacs are also absent from the Sail-fluke, a highly specialized Heterosomid, which lacks the "recessus orbitalis"† and has departed from the sand-loving habits of the other flat-fish. These facts lead to the conclusion that the presence of nasal "sacs" is

* In another species of the Sole-group, it was found that certain parasites (*Lernæa*?) had made their way into the nasal sacs and had caused a perforation of the roof of the mouth!

† *Cf.* Holt, E. W. L.: "Studies in Teleostean Morphology." Proc. Zool. Soc. 1894, p. 422.

an adaptation to semi-sedentary, as opposed to migratory, habits of life.

The function of these sacs in the first stage is moreover aptly described, as has been said, by the word "reservoir." In the tolerably quiet life these animals lead, the water containing odoriferous particles will not pass so freely over the olfactory epithelium as in the case of the free-swimming migratory forms. These sacs are, however, distended and constricted by the movements of the premaxillæ and maxillæ, and are thus able to draw in water, the odoriferous particles in this way coming into contact with the sensory epithelium without necessitating any movement on the part of the animal as a whole.

The second stage, where definite secretory sacs are present, has been found so far only in the family of the Heterosomata comprising the Halibut, Plaice, and Turbot groups. The secretion is forced from the sacs into the nasal cavity and over the sensory epithelium by the movements of the premaxillæ and maxillæ, in a fashion similar to the water in the previously described species.

The function of these secretory sacs is not very evident. They are absent in other Teleostei so far as is known, and this might mean that the olfactory organ is of little importance or that the epithelium is maintained sufficiently sensitive by water alone. In the air-breathing Vertebrates the nasal secretion is of importance in cleansing the organ, in keeping the sensory epithelium in a healthy sensitive condition, and in aiding towards bringing odoriferous materials into a state of solution favourable to their full appreciation. When the secretion is present in Fishes, therefore, it may signify that the olfactory organ is much used and of great importance. Such, indeed, would seem to be the case with the flat-fishes mentioned. In the life these animals lead as ground-feeders, searching for their food almost entirely by sense of smell, this secretion may be of as much service in cleansing the olfactory epithelium and maintaining it sensitive as the nasal secretion of the air-breathing Vertebrates.

In the Sole group the secretory has given place for the most part to a water-retaining function. This change might at first sight appear strange, as a return to a previous condition, although the animals are more sand-loving in their habits than even the Plaice, Halibut, and Turbot, and in most cases have their olfactory organs as largely developed as these forms. But the tactile sense, as shown in the development of papillæ and filamentous outgrowths * of the integument, here aids and even replaces the olfactory organ to a great extent. There is probably not the same necessity, therefore, for the epithelium to be kept in a high degree of sensitiveness as is the case with the Halibut, Plaice, and Turbot. Further, it is well known that a large quantity of mucus is secreted from the external surface in the Soles; and this, entering the nasal organ with the water-currents, may replace definite secretory sacs and effect the cleansing and preservation of the epithelium as efficiently as the needs and mode of life of the animals require.

When we come to *Cynoglossus*, we find the last stage in the structural specialization, apparently the complete return of the nasal "sacs" to the earliest function of water-retaining. The sacs are not secretory, and, further, there are no tactile filaments round the head; and it may be that the mucus from the skin enters the nasal cavity and acts as a nasal secretion, just as has been suggested for *Solea*.

In the divergent specimen of *Cynoglossus*, the perforation of the roof of the mouth brings into consideration a totally new function; but by the change that has occurred, the *raison d'être* of the former function of water-retaining is still as efficiently fulfilled. The odoriferous particles which the closed sacs induce to pass over the olfactory epithelium will be drawn through the nasal cavity during the process of respiration, by the movements of the mouth and gill-covers. The respiratory function, however, although it has arisen secondarily, probably becomes the more important.

The manner by which the Teleostean fishes respire has recently been carefully described by Dahlgren (*l. c.*), who shows what an important rôle is played by the maxillary and mandibular "breathing-valves" (fig. 4, *b.v.*). These are well-developed in the divergent specimen of *Cynoglossus*; but it is probable that in the mode of life which these animals lead, the circular fold beneath the central sac which receives the internal nares has taken the place of, or at least may act in the same manner as, the breathing-valves. Both would function when the animal's head was free in the water, but when the jaws were buried in the sand, the nasal respiratory canals and this "respiratory-fold"

* Raffaele, F.: "Papille e organi di senso cutaneo nei Pleuronettidi del genere *Solea*: nota preliminare." Naples, 1886.

would be most in action, opening and shutting synchronously with the gill-covers. When the gill-covers rise, and so increase the cavity of the mouth, whilst the posterior edges of the branchiostegal membranes close the gill-openings, this fold will also rise, and water will enter the mouth from the nasal passages. Conversely, when the gill-covers fall, the fold will press on the internal nares and close them; whilst the water from the mouth, passing between the gill-arches, bathing the gills, will escape by the gill-openings *.

The foregoing discussion of the functions of the nasal sacs and their specialization, leads on to a consideration of Huxley's conclusions with respect to the use of the communication between the nose and mouth in the fishes with which he dealt. In his paper on *Ceratodus* (l. c.), after comparing the Dipnoi and Selachii with regard to the nasal organ, he raised the question—of what use are such nasal passages and internal nares to purely branchiate animals? In answering this, he considered that in all probability they are primarily connected with respiration when the mouth is closed; and, secondarily, that by their means a constant stream of water containing odoriferous particles would be brought into contact with the sensory epithelium of the olfactory organs.

What has been advanced in the foregoing pages is so far in complete accord with both of these conclusions, but Huxley went beyond this and, reasoning from the second, concluded that the posterior nostrils of the Teleostei, where they occur, have most probably a function similar to the internal nares, viz., to aid in ensuring the adequate passage of odoriferous particles over the sensory epithelium.

This conclusion is, however, open to doubt. When internal nares are present, the pumping action which draws the water through the nasal passages is carried on by means of the gill-covers and floor of the mouth in common with that concerned in respiration. But in those Teleostei where internal nares and nasal sacs are absent and posterior nostrils are present, this pumping action during respiration cannot involve the olfactory organ. Hence the essential conditions which would render the

* Howes has proposed to distinguish this buccal mechanism of respiration characteristic of all the Ichthyopsida as *stomatophysous*, and that characteristic of the Amniota, and taking place only in the presence of a costal sternum, as *somatophysous*. *Cf.* Jour. Anat. & Phys. vol. xxiii. p. 272.

physiological significance of the posterior nostrils similar to that of the internal nares are absent.

The walls of the posterior nostrils, again, act as valves whose function is to let water pass from within outwards. In the free-swimming forms, therefore, when both nostrils are present, it is probable that the movements of the fish through the water suffice to induce the passage of water through the nasal cavity; and this flow is controlled by the anterior nostril, whose walls may be prolonged into a contractile tube or flap-like covering. Where only one external nostril is present, it is the anterior which must carry on the functions of the two of the other forms. And hence, if analogies are to be drawn, the anterior nostrils might be likened physiologically to the internal nares, and the posterior nostrils to the gill-openings. Similarly, when nasal sacs are present the displacement of the sacs ensures the circulation of water through the nasal cavity, just as the movements of the mouth and gill-covers cause the passage of water through the mouth, and the posterior nostrils are again only comparable to the gill-openings.

We may proceed now to a consideration of the other water-breathing Vertebrates in which the function of respiration is in part carried on by a naso-pharyngeal communication. In the Cyclostomes we find an analogy to what is seen in *Cynoglossus*. In the Petromyzontidæ there is a prolongation from the nasal cavity backward to the roof of the mouth; in the Myxinidæ the latter is pierced, and the communication thus opened is supposed to fulfil a respiratory function. The origin and development of this so-called prolongation of the nasal organ have been described by Dohrn * for *Petromyzon*, and recently somewhat briefly by Dean † for *Bdellostoma*.

Leaving aside the apparent remarkable differences alleged by Dean in the development of these two forms, it is clear that the internal nares of the Myxinidæ are formed by the communication of the hypophysis with the gut. According to Dean the hypophysis arises in *Bdellostoma* before the external openings of the

* Dohrn, A.: "Studien zur Urgeschichte des Wirbelthierkörpers. III. Die Enstehung u. Bedeutung der Hypophysis bei *Petromyzon Planeri*." Mitt. Zool. Stat. zu Neapel, 1883. *Vide* Howes, G. B.: "On the Affinities, Inter-relationships, and Systematic Position of the Marsipobranchii." Tr. Biol. Soc. Liverpool, vol. vi., 1891, p. 122.

† Dean (Bashford): 'On the Embryology of *Petromyzon Stouti*.' Kupffer's Festschrift, Jena, 1899, p. 269.

mouth and nose appear; and if this allegation should hold good also for *Myxine*, a special importance must be ascribed to such an early communication of the hypophysis with the gut, and it would furnish an argument in favour of Dean's view that the Myxinidæ and the Petromyzontidæ stand to each other in somewhat the same relation as the recent Selachians to the recent Ganoids. But, however widely they may be separated, the hypophysis would appear to present a condition analogous in the one group to that of the closed nasal-sac state aforementioned, and in the other to that of the open nasal canals in *Cynoglossus*.

The assertion of Dean that the hypophysis in *Bdellostoma* opens into the gut before the external opening of the nasal organ is formed, if correct, further leads to the conclusion that the so-called "internal nares" of the Myxinidæ, although a primary formation, is only secondarily connected with respiration. The reverse is the case in *Cynoglossus*, and thus there arises a good example of convergency in evolution, since a similar structure possessing a similar function, but having a totally different origin, would appear to have arisen in two separate groups of the animal kingdom.

On the other hand, there is so much diversity of opinion with regard to the development of the internal nares in the higher Vertebrates, that reference to them is somewhat difficult. According to Balfour's theory *, the nares arise from a single depression lying anterior to, and one on each side of, the mouth. This depression, as the embryo develops, takes the form of a longitudinal slit, and a little later passes through a stage similar to that of the adult Selachian. By the fusion of the adjacent tissues over the depression, this slit becomes tranformed into a canal with an opening at either end—these openings represent the external and internal nares. The later development differs in the different groups. In the Amniota, Balfour believed that the maxillary region of the face so develops in relation to the canal that the two openings become widely separated, the outer passing upwards and forming the external nares, the inner passing inwards and forming the internal nares. In the Amphibia it was believed that the origin of the internal nares is distinct from that above described, being "secondary," through perforation of the roof of the mouth after the latter is developed; and the development of the nares in the Dipnoi was considered to be similar to

* Balfour, F. M.: 'Comparative Embryology,' vol. ii. pp. 533–538.

that in the Amniota, except that the upward rotation of the external nostril does not take place. In the Teleostei, lastly, it was believed that the homology still holds good, and that both nares are rotated outward and upward. Hence the posterior nostrils of the Teleostei would be homologous to the external nostrils of the higher Vertebrates, and the anterior to their internal nares.

These generalizations have been in part confirmed and in part refuted by more recent workers. For the Teleostei, Sagemehl *, though believing that he was refuting Balfour's view, in reality corroborated it. For the Dipnoi, Semon † has shown that the nares develop as Balfour suggested; and he thus confirms Huxley's conclusions (*l. c.*), drawn from a comparison of the adult conditions, that, as concerning their nostrils, the Dipnoi and cartilaginous fishes are closely related. An important modification of Balfour's view has, however, to be noted. In the Dipnoi the communication between the nose and mouth is naso-labial, not naso-pharyngeal, the posterior aperture being morphologically disposed external to the teeth which arise on the vomer and palatine bones. Further, there is no true "palate"; and the question whether the maxillæ of fishes are truly homologous with the maxillæ of the higher Vertebrates is left open (Semon, *l. c.*, p. 45). As regards the internal nares, it is thus evident that no true homologue to that of *Cynoglossus* exists in the class Pisces.

In the higher Vertebrates, however, if the internal nares arise secondarily in the Amphibia, as suggested by Balfour, there is the possibility of such an homology. Hochstetter ‡, however, has thrown doubt upon the whole of Balfour's conclusions with regard to the origin of the internal nares in the Amniota. He shows that the "palate" is not formed by the maxillary bones, but by the fusion of the external and median primitive nasal processes, and that the internal nares then arise secondarily by the perforation of the palate. These observations were made upon certain mammalian forms; and in the same forms as well as

* Sagemehl, M.: "Das Cranium von *Amia calva*, L." Morph. Jahrbuch, Bd. ix. p. 221.

† Semon, R.: "Die äussere Entwickelung das *Ceratodus Forsteri*." Denksch. der Med.-Naturwiss. Gesellsch., Jena, Bd. iv. 1893, pp. 44–45.

‡ Hochstetter, F.: "Ueber die Bildung der inneren Nasengänge oder primitiven Choanen." Verh. d. Anat. Gesellsch. 1891 (Anat. Anz. Bd. vi Suppl.) p. 145.

in others Keibel * has more recently, in opposition to His †, confirmed those which concern the formation of the palate, though he is doubtful about the secondary origin of the internal nares.

If the conclusions of Hochstetter had been the last word on the matter, it would have been possible to frame an homology between the internal nares of *Cynoglossus* and those of the higher Vertebrates. If the latter arise secondarily in ontogeny, then it is probable that at their first beginning they were also of secondary origin, and therefore distinct from the primitive internal nares of the Dipnoi. Hence we might have in *Cynoglossus* a glimpse of what may have occurred at a remote period of time, when the air-breathing Vertebrates were but in process of evolution.

But if Keibel's suggestions (see footnote ‡) are well-founded, then we must accept, in a modified form, Balfour's view concerning the origin of the internal nares as the true one, and upon this no comparison could be made between *Cynoglossus* and the higher Vertebrates. Morphologically, *Cynoglossus* would then be perfectly unique, possessing not only the homologues of the internal nares in the morphological sense, but additional organs also which represent the internal nares in the physiological sense. The internal nares of *Cynoglossus* should then be called "pseudo-nares" or "pseudo-choani," which would emphasize their morphological distinction from the "choani" of the higher Vertebrates, whilst implying their physiological similarity.

It is of interest to note, in conclusion, that this discovery in the Teleostei of a distinctive peculiarity of the higher Vertebrates, is not without a parallel. Warm blood has been found in the

* Keibel, F.: "Zur Entwickelungsgeschichte und vergleichenden Anatomie der Nase u. des oberen Mundrandes (Oberlippe) bei Vertebraten." Anat. Anz., Bd. viii. 1893, p. 473.

† His, W.: "Die Entwickelung der menschlichen und tierischen Physiognomieen." Archiv f. Anat. u. Phys. (Anat. Abth.), 1892, p. 399.

‡ In his short paper Keibel concerns himself mostly with the palate and upper lip of the Vertebrates, and it is only secondarily that he throws out suggestions as to the formation of the internal nares. Hence his meaning is not very easily determinable, but it seems to be as follows:—The internal nares are homologous and primary structures wherever they appear in the Vertebrate kingdom. They arise from the inner portion of the primitive nasal groove—as described by Balfour—but instead of the maxillæ growing in between the primitive nostril and nares, it is the "palate"—formed from the median and external primary nasal processes. The Selachii represent, therefore, the most primitive condition, where the primary nasal groove persists.

Tunny, viviparity occurs in *Zoarces* and in other Teleosts; and in *Anableps* it is said that "the vascular yolk-sac is provided with villi which absorb nutriment" from the fluid secreted by the walls of the dilated ovary within which the embryo develops *. The Elasmobranchs offer numerous instances of this kind; and Professor Howes (who has aided me liberally with the literature throughout my work) has at the last moment drawn my attention to another case which compares in its "uniqueness" with the divergent specimen of *Cynoglossus*. In the Anurous Amphibia he has shown † that the epiglottis—an accessory voice-organ peculiar to Mammals—is of frequent occurrence in an elementary form, liable to great individual variation. In *Chiroleptes australis* the epiglottis was developed in one specimen, a male; in another, also a male, it was insignificant; whilst in a third, a female, the epiglottis was small and the accompanying "epilaryngeal folds" absent. He informs me that three more adults, which he has examined since his paper was written, were wholly destitute of the organs in question. So far, therefore, only one specimen of this species has been found with these organs well-developed. With the exception perhaps of this last case, the foregoing are all examples of separate specializations in the respective modes of life of the animals, and show once more how plastic is the organism in the grasp of its environment.

EXPLANATION OF PLATE 38.

Fig. 1. Semidiagrammatic transverse section across the nasal region of a Pleuronectid (Plaice or Halibut), to show the nasal secretory sacs, $n.s._1$—$n.s._4$.

The Dipnoi occupy the second stage, where a rudimentary true palate is represented by the hinder portion of the upper lip anterior to the teeth, but where no true maxillæ are developed. The palate (?) is here formed by the nasal processes (*cf.* Semon, *l. c.*), and the naso-pharyngeal communications arise from the primary nasal grooves. The Amniota show the third and last stage. The palate and the internal nares are formed as above, and the maxillæ grow round anteriorly to complete the external boundaries of the mouth.

* Haddon, A. C.: 'The Study of Embryology,' p. 98. (*Cf.* Wyman—Boston Journ. Nat. Hist. vol. vi. p. 432.) My best thanks are due to Mr. A. W. Kappel, the resourceful Librarian of the Linnean Society, for the pains with which he has determined this reference.

† Howes, G. B.: "On an unrecognized feature in the Larynx of the Anurous Amphibia." Proc. Zool. Soc. 1887, p. 497.

Fig. 2. Semidiagrammatic longitudinal section through the skull of *Solea lascaris*, to show the nasal sacs, *r.n.s.* and *l.n.s.*

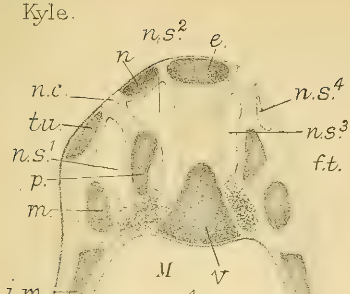
3. *Cynoglossus semilævis*: a dissection from the left side, showing the left olfactory organ (*o.l.*), the mandibular tooth-mass of the right side (*t.m.*), and indicating, diagrammatically in dotted lines, the course of the left naso-pharyngeal canal (*n.p.c.*), and the position of the aperture of the naso-pharyngeal sac (*c*).

4. The same: ventral view of the roof of the mouth, showing the aperture of the naso-pharyngeal sac (*c*), and, diagrammatically in dotted lines, the course of the naso-pharyngeal canals (*n.p.c.*). The arrows point towards the internal openings.

5. The same: a dissection to the level of the naso-pharyngeal sac, the left wall of which (*c.f.*) has been turned outwards to show the course of the left naso-pharyngeal canal (*n.p.c.*), and the slit-like expansion of the naso-pharyngeal canal of the right side (*n.c.*) as it opens into the sac (*c*).

Reference Letters.

b., basioccipital.
b.v., breathing-valves.
c., sac in roof of mouth into which the naso-pharyngeal canals open.
c.f., cut edge of fold round sac (*c*).
e., ethmoid.
e.l., left eye (displaced).
e.o., opening of naso-pharyngeal canal into nasal cavity.
f., fold round naso-pharyngeal sac (*c*).
fr., frontal.
f.t., fatty tissue.
h., hyomandibular.
i.m., premaxilla.
l.n.s., left nasal sac.
l.i.m., left premaxilla.
l.m., left maxilla.
m., maxilla.
M., mouth.
md., left mandible.
mt., metapterygoid.
n., nasal bone.
n.c., nasal cavity.
$n.s._1$—$n.s._4$, nasal sacs.
n.p.c., naso-pharyngeal canal.
o.l., left olfactory organ.
op., operculum.
p., palatine.
p.o., preoperculum.
pr., prootic.
p.s., parasphenoid.
qu., quadrate.
r.i.m., right premaxilla.
r.u., right maxilla.
r.n.c., opening of right naso-pharyngeal canal into sac (*c*).
s.o., supraoccipital.
t.m., tooth-mass of right mandible.
tu., turbinal.
v., vomer.



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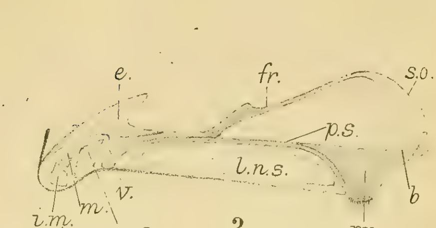

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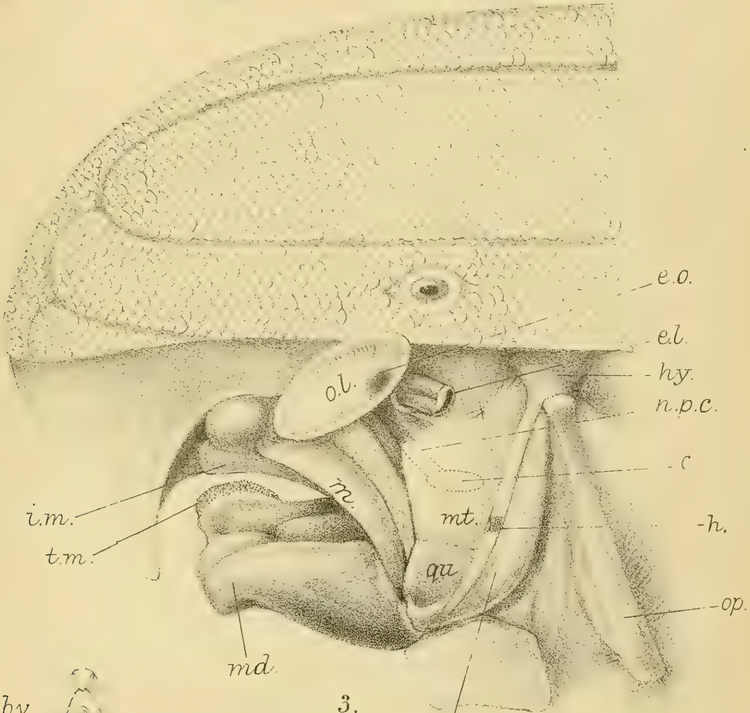

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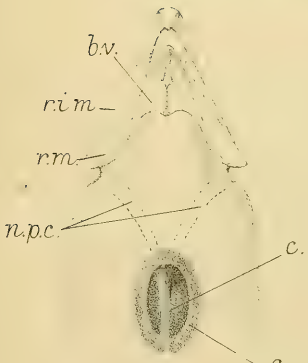

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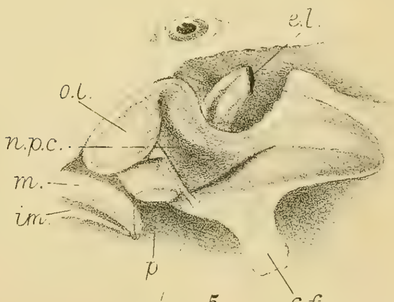

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H.M.K. del.
J. Green lith.
Mintern Bros. imp.

NASAL SACS IN TELEOSTEANS.